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BALLISTIC CONTRACTIONS IN MAN: CHARACTERISTIC RECRUITMENT PATTERN OF SINGLE MOTOR UNITS OF THE TIBIALIS ANTERIOR MUSCLE

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SUMMARY

1. Single motor units were recorded with highly selective electrodes from intact tibialis anterior muscle in the adult man. A detailed parametric analysis was made of the discharge patterns during voluntary isometric contractions of different peak forces carried out at various rates of force development.

2. During the smooth tracking of a ramp force, the different motor units recorded from a given muscle site were recruited in a consistent order, each unit becoming active when the muscle developed a certain level of force. The threshold of some of the units in such slow ramp contractions exceeded 8 kg. By contrast, in brisk ballistic contractions reaching a peak force of 12 kg in less than 0·15 sec, the same motor units discharged in a transient burst which largely preceded the muscle force production.

3. In slow tracking ramp contractions, the instantaneous frequency of single motor units was initially rather low (5–15/sec) and it increased as the ramp force augmented. By contrast, in (strong) ballistic contractions, the same units discharged at an unusually high instantaneous frequency (60–120/sec) early in the burst and the firing frequency decreased thereafter. Such hitherto unknown pattern appears characteristic of ballistic contractions and it was not found in even fast tracking ramp contractions achieving 12 kg in only 0·4 sec.

4. The potentials of the different motor units activated are rather crowded at intervals of a few msec in the early burst of a strong ballistic contraction and observations on the rank activation of the different motor units do not provide reliable data for the analysis of the recruitment order of units in ballistic contractions.

5. A new method is described for estimating ballistic force threshold of single motor units. When a large series of brisk ballistic contractions with peak forces ranging from 0·05 to 12 kg was carried out any given motor

unit only became active when the ballistic peak force exceeded a certain reproducible value. A detailed analysis of the recruitment order based on these ballistic force thresholds showed it to be virtually identical to the recruitment order of the same units in slow tracking ramp contractions (correlation = 0·95).

6. Ballistic contractions are graded in force both by the recruitment of additional motor units in stronger contractions, and by an increase in their rate of firing. These gradation mechanisms are discussed.

INTRODUCTION

Henneman's principle of an orderly recruitment of single motor units in movements of increasing force (Henneman, Somjen & Carpenter, 1965; Henneman, Clamann, Gillies & Skinner, 1974) is now well documented for human muscles when the subject smoothly tracks a slow ramp (Tanji & Kato, 1973; Milner-Brown, Stein & Yemm, 1973*c*; Freund, Büdingen & Dietz, 1975). The situation is less clear and sometimes even contradictory for fast movements and claims have been made that the sequence of activation of different motor units might be modified or even reversed in brisk voluntary movements (Grimby & Hannerz, 1968, 1973; Hannerz, 1974). It is well known that mammalian muscles contain twitch motor units with shorter and longer contraction times (Andersen & Sears, 1964; Henneman *et al.* 1965; Burke, 1973; Buchthal & Schmalbruch, 1970; Milner-Brown, Stein & Yemm, 1973*a*, *b*) and the question has occasionally been asked whether the faster contracting motor units might not be perhaps preferentially recruited in brisk movements. There is evidence for a different central organization of motor control for smooth ramp movements and brisk ballistic movements respectively (Kornhuber, 1971, 1974; DeLong & Strick, 1974; Thach, 1975) but this does not imply that, at the level of the spinal motoneurones, the recruitment order should necessarily be different.

This paper analyses in detail the activation pattern of single motor units in the tibialis anterior of normal adult subjects. Monosynaptic cortico-motoneuronal synapses (Phillips, 1969) have been demonstrated for lumbar motoneurones (Kuypers, 1960, 1973; Porter & Hore, 1969). The tibialis muscle which operates at a joint with one degree of freedom is able to execute very fast movements. Another reason for choosing the tibialis anterior was that Grimby & Hannerz (1973) described reversals of the recruitment order of motor units in fast movements of that very muscle. The present paper attempts to answer the following questions. (*a*) Are there different patterns of motor unit activation in smooth pursuit ramp movements and in ballistic movements respectively? (*b*) What is the recruitment order of simultaneously recorded motor units in these two types of movements? (c) What are the mechanisms for gradation of muscle force in the ballistic contractions?

METHODS

Five normal unpaid male volunteers between 21 and 29 years old were studied. A total of ninety-three single motor units were investigated in detail in the tibialis anterior muscle during voluntary contractions as follows: (a) several ramp contractions at different rates which achieved 12 kg isometric force in chosen times ranging from 10 to 0·4 sec; (b) several ballistic contractions of 12 kg peak force performed as fast as possible, followed by relaxation; (c) at least fifty ballistic voluntary contractions performed as fast as possible, but achieving different peak forces ranging between 0·05 and 12 kg. The motor units considered in this paper were those which could be clearly identified from the background throughout these various tests.

Motor unit recording. Highly selective electrodes made with 40 μm diamel coated nichrome wire were inserted into the proximal 7 cm of the tibialis anterior belly; either closely adjoining wires inserted in a curved hypodermic needle (Desmedt & Godaux, 1975), or a light-weight concentric needle of 2 cm length which was constructed with a 40 μm diameter nichrome were used. The 40 μm wires serving to connect the electrodes to the preamplifier were highly flexible which minimized any movement of the electrode tip with respect to the motor units even during brisk movements. The use of highly selective electrodes and their careful positioning into an

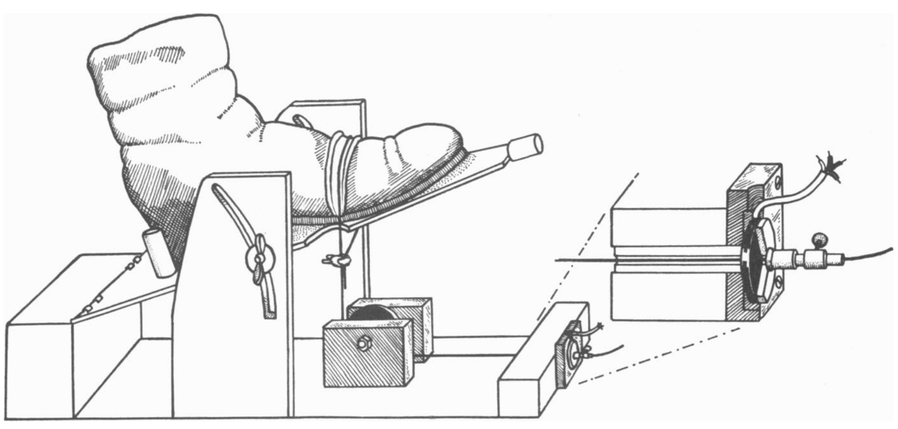

Fig. 1. Diagram of the experimental set-up for studying single motor units in the tibialis anterior muscle. The heavy leather shoe rests on an adjustable footplate. The steel wire passing over the bracket compresses the gauge which is seen in semi-exploded view (black) in its lodging on the right side.

appropriate area of the tested muscle allowed to reliably identify for a single electrode position, several motor unit potentials from their characteristic and consistent wave forms, throughout the whole range of increasing muscle force. Electrode placements for which the motor unit potentials studied underwent distortions or interferences from other motor units during strong contractions were discarded. As a rule, the potentials (0·5–2·0 mV) of one to five different motor units could be studied reliably with the above programme at any such appropriate position. The potentials were amplified by a 20 MΩ input impedance differential preamplifier and displayed on Tektronix 565 and Hewlett Packard 1201B cathode-ray oscilloscopes. The system bandpass was restricted to 0·1–5 kHz which proved adequate to consistently identify the different units wave forms. The traces were intensified in their vertical moves by Z modulation and photographed with a Grass C4 camera on 35 mm film. The motor units were stored on a Hewlett Packard 4-channel FM magnetic tape recorder operated at 15 in./sec.

Force recording. The subject was comfortably seated in a chair while the foot rested on a stable metal footplate with the ankle at 90°. A metal harness 2 cm wide rested on the foot dorsum over the distal part of the first metatarsal bone; it was connected through 0·8 mm diameter steel wire over a pully (with ball bearings) to an ELF-1000-250 Flatline load cell mechanical transducer (Fig. 1). The compliance of this gauge was about 0·1 mm for the full range of 125 kg. The subject was wearing thick leather shoes to avoid any local pain during the strong dorsiflexions of the foot. In order to minimize distortions of the isometric myogram by extraneous series elastic components, the footplate was adjusted and locked firmly in such position that the harness pressed the foot on to the footplate with a force of 10 kg when the muscle was relaxed. Very small contractions producing only a few grams could then be reliably recorded. The mechanical system was linear from 5 to 90 kg and it was calibrated with weights after each experiment. The natural frequency of the transducer when loaded by the bracket was 400 Hz.

The subjects received no special instructions about the auditory feed-back of the motor unit potentials discharges provided. They looked at a Tektronik 565 oscilloscope screen with persistent trace which displayed the force record. They were asked to contract the tibialis muscle so as to track ramps of appropriate slopes calibrated in kg per second. The isometric myogram was stored on one channel of the 4-channel FM tape recorder. The intramuscular temperature was monitored with a thermistor needle and maintained at 36–37° C by infra-red heating when necessary.

RESULTS

When the subject contracts the tibialis anterior muscle in order to track a rather slow force ramp with a slope of about 2 kg/sec, there is an

Fig. 2. Transverse oscilloscope sweeps photographed on film running from above downwards. The continuous line is the isometric force record in which the force moves the non-sweeping oscilloscope spot to the right. The recording method allows several single motor units to be safely identified by their characteristic wave forms. There is slight fluctuation in the peak voltage. *A–C*, segments of film recorded during a smooth ramp contraction achieving a force of 6·4 kg in 5·2 sec. *A*, threshold activation of the first motor unit when the ramp force reaches 0·3 kg (unit marked 1). *B*, threshold activation of the second motor unit at 1·65 kg. *C*, threshold activation of the third motor unit at 3·9 kg. *D*, ballistic contraction reaching 6·4 peak force in 0·12 sec. The same motor units are recruited in the same order in the burst which starts before the force ouput. *E*, subsequent ballistic contraction of same force in which the same three motor units were recruited in a different sequence. The vertical and horizontal calibrations are the same for *A–E*. *F*, complete display of the isometric myogram of the ramp contraction in *A–C*, but on a slower time base. The force threshold of the three motor units are indicated by arrows. *G*, similar display on the same slow time base of the ballistic contraction in *D*.

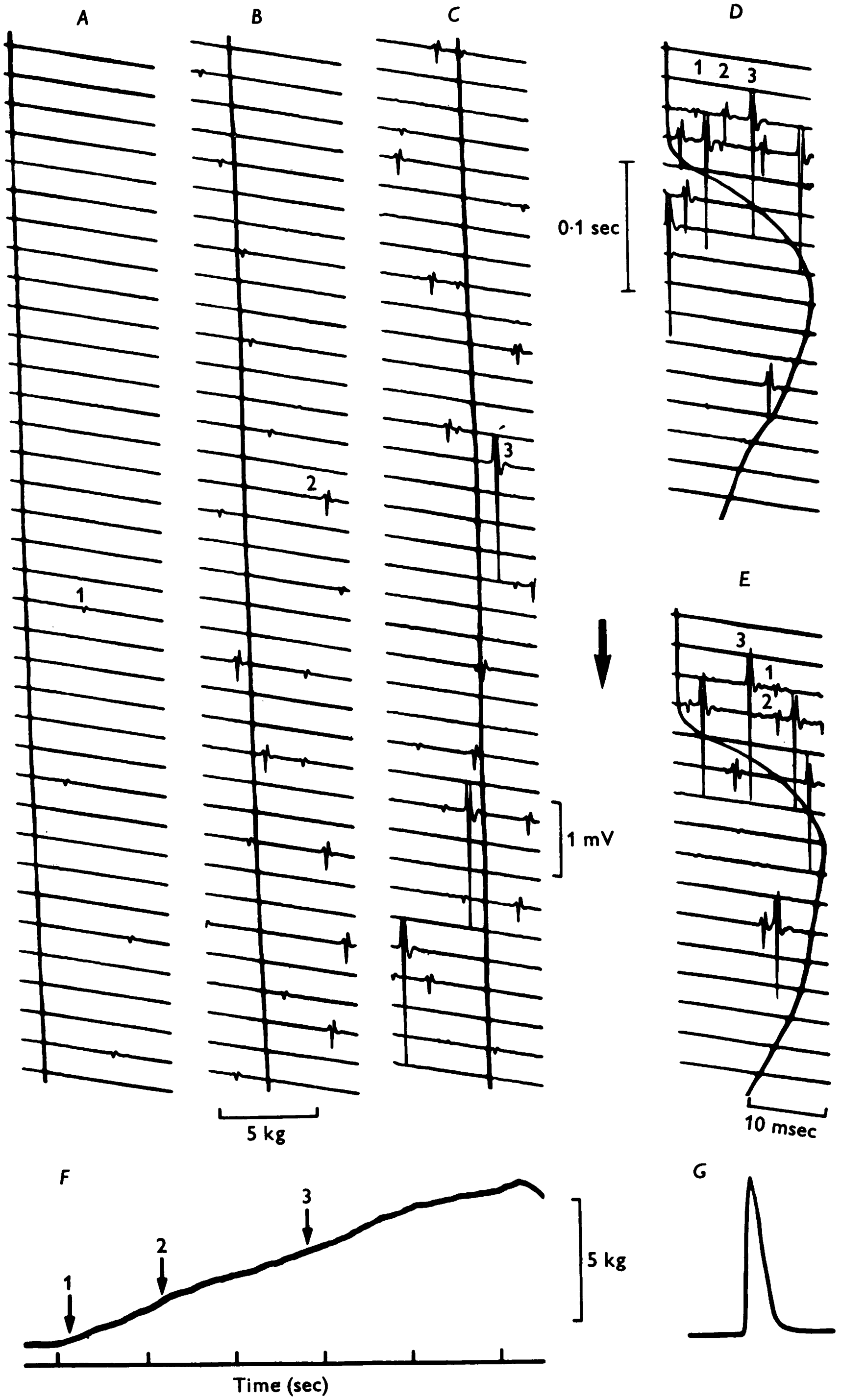

Fig 2. For legend see facing page.

orderly recruitment of the different motor units recorded from the same site, each unit becoming active at a fairly reproducible level of force. This is concordant with findings in other human muscles (Tanji & Kato, 1973; Milner-Brown *et al.* 1973*c*; Freund *et al.* 1975). For example, the first three units in the experiment of Figs. 2 *A–C* were recruited as the ramp contraction reached 0·3, 1·65 and 3·9 kg respectively. On the other hand, when the subject contracted his muscle as fast as possible, and produced a ballistic contraction, the same motor units were activated in a transient burst which started before the muscle actually produced any force. Each unit only discharged once or a few times in the burst. The time to peak of the ballistic contraction was about 0·13 sec.

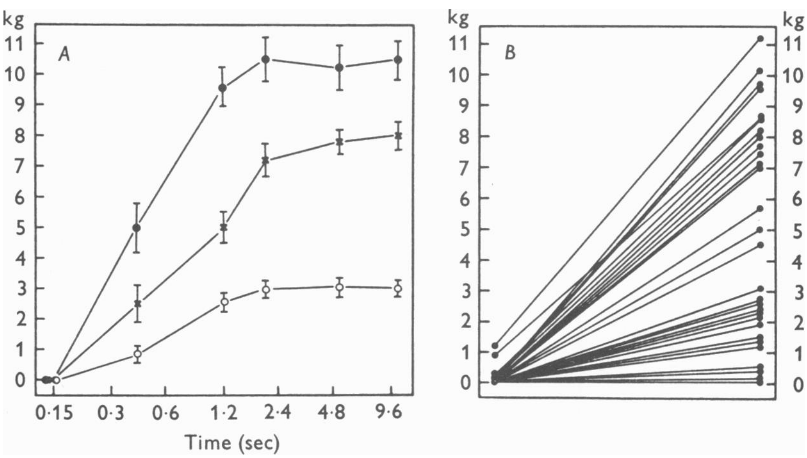

Fig. 3. *A*, force threshold for activation (ordinate) of three different single motor units as a function of the time to peak of the voluntary contraction (abscissa). The vertical lines correspond to ± 1 standard deviation about the mean calculated on ten trials. The thresholds decrease for ramp achieving the force of 12 kg in less than 2 sec, and they become zero for the ballistic contractions with time to peak below 0·15 sec. *B*, force thresholds activation of twenty-nine single motor units in smooth ramps of 12 kg in 5 sec (on the right side) and in ballistic movements of 12 kg in 0·12 sec (left side).

When a large number of ballistic contractions are studied for the same recording electrode position, the different motor units started firing according to the same order in which they had been recruited in slow ramp contractions (Fig. 2*D*). However, it must be said that a unit sometimes started discharging before another one which had been recruited at larger ramp force (Fig. 2*E*). Such occasional 'reversals' in brisk contractions (cf. Grimby & Hannerz, 1973) were by no means a consistent nor a steady feature of particular motor units. We compared thirty-six pairs of single motor units in about six strong ballistic contractions, each achieving a peak force of 12 kg and only found twenty such 'reversals' in the total of 186 paired samples (about 11 %).

Moreover, it must be emphasized that the early discharge of the motor units in ballistic contractions is quite dense and only a few msec intervene between the onset of firing of the different motor units so that the significance to be attached to such occasional earlier firing of one motor unit ahead of another one in the burst appears rather limited. Therefore, we tried to resolve this problem by developing an appropriate method to determine the ballistic thresholds and recruitment order of the motor units (see below).

The twenty-nine units plotted in Fig. 3*B* presented, in a slow ramp contraction, force thresholds which ranged between 0·03 and 11·2 kg. Twenty-five of these units were thrown into action in the ballistic contraction before the muscle actually developed any recordable force. The four remaining units only became active after the muscle had developed some ballistic force (0·06–1·3 kg) and they were rather high thresholds units since, in slow ramp contractions, they had only been recruited when the muscle produced force exceeding 8 kg.

Ramp contractions at various speeds and ballistic contractions. The rather marked differences found in recruitment pattern of motor units between a slow ramp contraction and a brisk ballistic contraction raise the question whether the 'ramp pattern' is maintaned or not in tracking contractions carried out at increasing fast rates. When the subject produced ramp contractions reaching 12 kg in 10 or in 5 sec, thus at rates ranging from 3 to 6 kg/sec, the threshold force at which any given unit was activated was not significantly different ($P > 0·07$) (Fig. 3*A*) (cf. Tanji & Kato, 1973). For faster ramp contractions of the tibialis muscle achieving 12 kg in less than 2 sec, the threshold force was clearly decreased (cf. Freund *et al.* 1975), but it remained at a definite level of force (Fig. 3*A*) even when the tracking contractions were carried out so fast as to reach in only 0·5 sec the peak force of 12 kg, that is about half maximum force of the muscle. Such rather fast tracking ramp contractions failed to involve the initial burst pattern found in non-tracking ballistic contractions reaching the 12 kg peak force in 0·11–0·16 sec, in the tibialis.

The contrast between even a fast tracking ramp and a ballistic contraction was further documented by analysing the mean instantaneous frequency of firing of single motor units. The latter was estimated from oscilloscope traces of the isometric force and of single motor unit potentials filmed at a camera speed 1 m/sec, in order to clearly identify the details of units' wave forms and to obtain precise time relations with the force. The instantaneous frequency of a unit at any chosen force level was taken as the reciprocal of the interval between two action potentials discharging at that

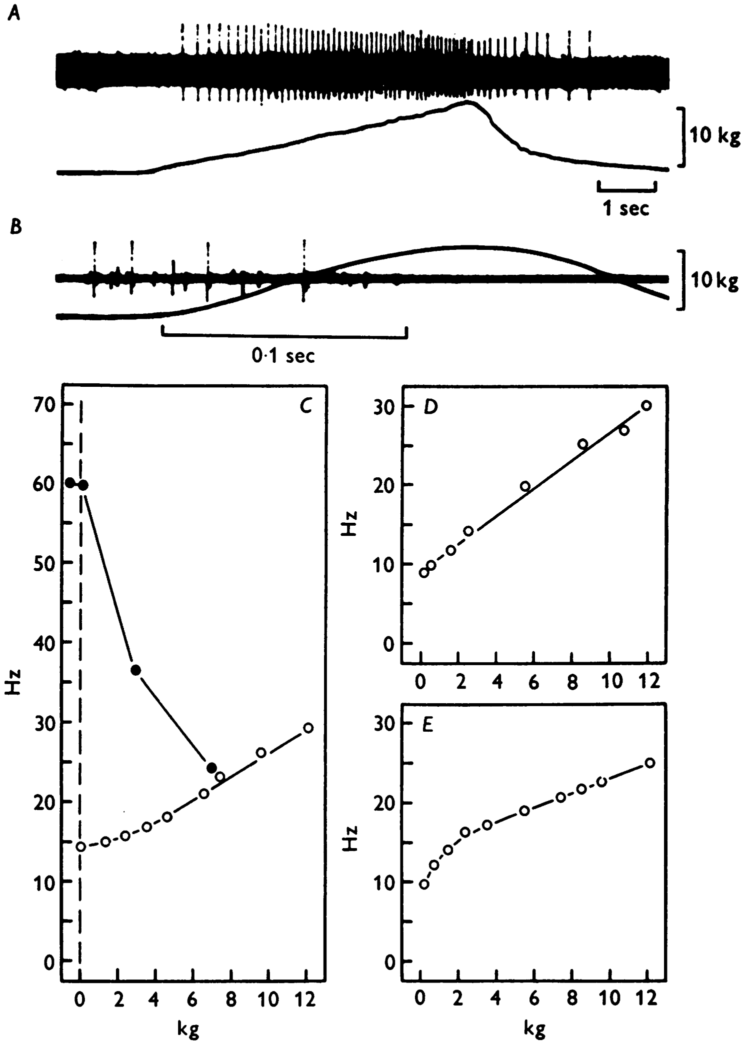

Fig. 4. Firing pattern of a single motor unit in a smooth ramp contraction of 12 kg in 5 sec (*A*) and in a ballistic contraction of 12 kg in 0·11 sec (*B*). Notice the difference in time scales. This unit was chosen because it was well isolated from the background in order to provide a clear display. *C–E*, mean instantaneous frequency of the same motor unit (ordinate) throughout the smooth ramp contraction (circles) of 12 kg carried out either in 1 sec (*C*) or in 5 sec (*D*), or in 10 sec (*E*). Abscissa, isometric force in kg. The filled circles in *C* correspond to the mean instantaneous frequency calculated on five consecutive ballistic contractions of 12 kg in 0·11 sec. Notice the high initial instantaneous frequency.

force. Several successive trials were studied to obtain five to ten separate estimates of such intervals at any force level considered.

Fig. 4 illustrates typical findings for one motor unit which was consistently recruited at 0·54 kg in a slow ramp contraction. For a ramp reaching 12 kg in 5 sec, the unit frequency was 9/sec at onset of firing and it increased roughly linearly up to about 30/sec as the ramp contraction developed more force (Fig. 4*A*, *D*). With a slower ramp reaching 12 kg in 10 sec (*E*) the graph presented an upward convexity, while with a faster ramp reaching 12 kg in 1 sec (*C*) the same unit started firing at 14/sec and the graph disclosed a slight upward concavity. Such features are consistent with those found in the first interosseus muscles by Milner-Brown *et al.* (1973*c*, Fig. 4). By contrast, when the subject produced a brisk ballistic contraction of the tibialis, the meán instantaneous frequency of the same motor unit was as high as 60/sec when calculated for the two intervals of the unit's first three discharges at the beginning of the ballistic burst (Fig. 4*C*). Fig. 4*B* shows one of the original traces on which this mean was calculated. As could be anticipated from the pattern seen in Fig. 2*D*, *E*, the intervals increased and the mean instantaneous frequency rapidly dropped for the subsequent discharges of the motor unit as the ballistic contraction developed.

The mean instantaneous frequency for twenty-four different motor units ranged from 60 to 120/sec in the early burst characteristic of ballistic contractions of the tibialis, and there was always a subsequent drop in instantaneous frequency in the later part of the burst. This pattern is genuinely different from the one observed when the subject tracked ramps in which case there was a progressive increase of the unit's frequency from an initial value of 5–15/sec, as shown in Fig. 4*C*. The latter ramp pattern was observed even for faster ramps achieving their peak in, say, 0·36 sec. It was only when the subject contracted the tibialis muscle as fast as possible without attempting any tracking that the ballistic pattern was achieved with a very high initial firing frequency exceeding 60/sec, which rapidly dropped to lower figures.

Estimation of the ballistic force threshold of a motor unit. The strong ballistic contractions of 12 kg so far considered involved a burst of many motor units, most of which discharged before any force was actually produced and we came to be convinced that the temporal order of discharges of the units in the first 15–40 msec of that burst provided no foolproof evidence for establishing the true recruitment order of these units. Therefore a new method was advised which proved highly consistent.

The subject carried out, at easy intervals of several sec, at least fifty ballistic contractions achieving a wide variety of peak forces which ranged from 0·05 to 12 kg. The weaker and stronger contractions were made in roughly random order to minimize systematic deviations. The subject was instructed to produce a brisk contraction immediately followed by a relaxation. A given level of ballistic peak force could only be achieved after several trials which allowed the subject to adjust his voluntary commands by successive approximation. The subject could then reproduce fairly

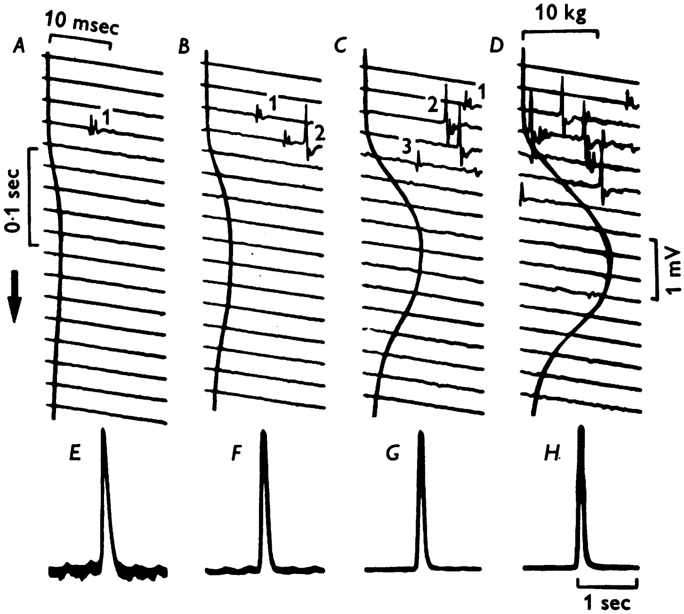

Fig. 5. Ballistic contractions with times to peak of 0·11 sec and with different peak forces of 1·4 kg (*A* and *E*), 3·6 kg (*B* and *F*), 6·3 kg (*C* and *G*) and 10·1 kg (*D* and *H*). Same display as in Fig. 2. The contractions are also presented on a slower time base in the lower row of records in which the vertical amplifications were adjusted to obtain similar sizes for the very different peak forces of these ballistic contractions, thereby showing their similar profile. The oscillations of the base line at higher amplification in *E* and *F* correspond to interference from arterial pulsations.

accurately the same ballistic force in a series of contractions carried out at 5–10 sec intervals. Adjustment of the commands were again required for other levels of force, which is not surprising since the tibialis anterior is not usually involved in the production of small accurate ballistic contractions. Many trials were carried out in order to secure a complete series of fifty specimens closely covering the entire range of ballistic forces. After the experiment, the taped data were filmed in displays similar to those of Fig. 2*D*. Two film records were obtained for any one ballistic contraction in order to check that no action potential had been missed on the trace at the beginning or end of the (transverse) oscilloscope free-running sweeps.

This method allowed a detailed study of wave forms of potentials, while saving film and the precise time relation with respect to the force record were not a primary consideration in this part of the work (see above).

Fig. 5 shows four samples of records in a typical experiment. The ballistic contractions of different force reached their peak in less than 0·15 sec

TABLE 1. Motor unit threshold data

Trial	Force (kg)	Units 1	2	3	4	5	Trial	(kg)	Units 1	2	3	4	5
1	0·07	+	−	−	−	−	27	2·27	+	+	+	−	−
2	0·08	+	−	−	−	−	28	2·42	+	+	+	−	−
3	0·15	+	−	−	−	−	29	2·72	+	+	+	+	−
4	0·30	+	−	−	−	−	30	2·75	+	+	+	−	−
5	0·30	+	−	−	−	−	31	3·18	+	+	+	+	−
6	0·31	+	−	−	−	−	32	3·20	+	+	+	−	−
7	0·31	+	−	−	−	−	33	3·33	+	+	+	+	−
8	0·37	+	−	−	−	−	34	3·48	+	+	+	+	−
9	0·38	+	−	−	−	−	35	3·51	+	+	+	+	−
10	0·45	+	+	−	−	−	36	3·78	+	+	+	+	−
11	0·46	+	+	−	−	−	37	4·54	+	+	+	+	+
12	0·53	+	−	−	−	−	38	4·84	+	+	+	+	+
13	0·75	+	+	−	−	−	39	4·99	+	+	+	+	+
14	0·90	+	+	−	−	−	40	5·15	+	+	+	+	+
15	0·90	+	+	−	−	−	41	5·30	+	+	+	+	+
16	0·91	+	+	−	−	−	42	5·45	+	+	+	+	+
17	1·06	+	+	−	−	−	43	5·75	+	+	+	+	+
18	1·06	+	+	−	−	−	44	6·96	+	+	+	+	+
19	1·06	+	+	−	−	−	45	8·03	+	+	+	+	+
20	1·14	+	+	+	−	−	46	8·10	+	+	+	+	+
21	1·21	+	+	+	−	−	47	8·18	+	+	+	+	+
22	1·36	+	+	−	−	−	48	8·63	+	+	+	+	+
23	1·38	+	+	+	−	−	49	9·54	+	+	+	+	+
24	1·51	+	+	−	−	−	50	9·69	+	+	+	+	+
25	1·81	+	+	+	−	−	51	10·90	+	+	+	+	+
26	1·82	+	+	+	−	−	52	12·70	+	+	+	+	+

even at extremes of the range. The lower row of isometric myograms (presented with vertical amplification reduced roughly proportionally to the increase in force) indicates a similar profile of mechanical tension development for ballistic contractions producing from 1·4 to 10·1 kg peak force. The ballistic force threshold can be defined because there is a consistent recruitment of additional motor units for definite increment of peak force. Thus unit no. 2 which did not discharge in Fig. 5*A*, has reached its threshold in *B*, where unit no. 1 is now seen to discharge twice. Unit no. 3 fired in the ballistic contractions of 6·3 kg peak force in *C*, in which units nos. 1 and 2 discharged twice each. An even stronger contraction of 10·1 kg peak in D involved four discharges of units nos. 1 and 2 and three discharges of unit no. 3.

The ballistic threshold of any one motor unit was determined after ranking these data according to increasing peak force, irrespective of the actual order in which the different ballistic contractions had been made by the subject during the experiment. A given motor unit failed to be activated in all the contractions below a certain peak force; it discharged with increasing probability for slightly stronger contractions, and then fired with no failure in all the ballistic contractions producing a still larger force (Table 1). The ballistic force threshold was estimated by taking the

TABLE 2. Motor unit threshold

	Ballistic force threshold (kg)		Ramp force threshold (kg)	
Unit	Range	Mean	Range	Mean ± S.D.
1	0–0·07	0·035	0·14–0·48	0·34 ± 0·15
2	0·38–0·75	0·56	3·50–4·10	3·70 ± 0·28
3	1·06–1·81	1·43	3·60–4·40	4·14 ± 0·36
4	2·72–3·33	3·02	11·98–13·15	12·66 ± 0·57
5	3·78–4·54	4·16	13·73–16·41	15·46 ± 0·93

mean between the maximum peak force for which that unit never discharged and the minimum peak force for which it always fired. Table 1 shows data for five different motor unit potentials recorded from the same site in the same experiment, during fifty-two trials with peak forces ranging from 0·07 to 12·70 kg. Unit no. 1 discharged securely from the smallest contractions which could be measured, only 0·07 kg peak force; since it was not spontaneously active, its mean ballistic threshold was (arbitrarily) taken at half that value, thus 0·035 kg. Unit no. 2 did not discharge up to a ballistic contraction of 0·38 kg and it fired securely at 0·75 kg and above. Its mean threshold was thus considered as 0·56 kg. The ballistic threshold of the units can be compared with their threshold in ramp contractions (Table 2), the latter being estimated from the data of ten separate ramp contractions producing 12 kg in 8 sec.

Recruitment order of motor units in ballistic and ramp contractions. Detailed determinations of the force thresholds in graded ballistic contractions are available for sixty-four different tibialis motor units for which the force threshold in a slow 12 kg ramp has also been estimated. The data plotted in Fig. 6 indicate that the ballistic motor command involves a substantial reduction of the force threshold of all the unit studied. The reduction appears roughly proportional and the units with a higher ramp threshold tend to also present a larger ballistic threshold. A highly consistent linear relation was calculated with the function: $y = 0{\cdot}07 + 0{\cdot}28x (r = 0{\cdot}92)$.

The force threshold can thus be said to be reduced by a mean factor of about 0·7 when a given unit of tibialis anterior is activated in the ballistic mode instead of the slow tracking ramp mode. This finding suggests a general coherence in the activation pattern of the population of spinal motoneurones in either the ramp or the ballistic modes.

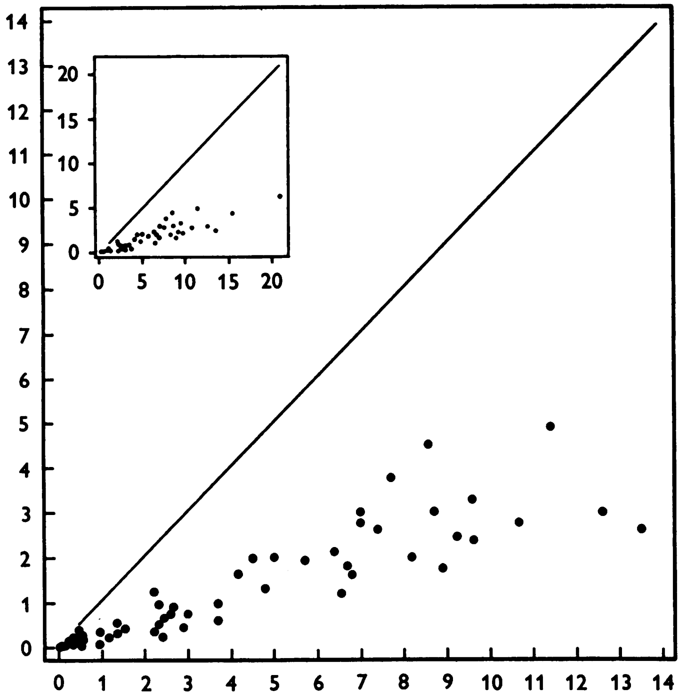

Fig. 6. Relation between the threshold for activation in a smooth ramp contraction (abscissa) and the ballistic force threshold determined from graded ballistic contractions, as described in the text (ordinate) for sixty-four single motor units. Sixteen points are crowded near the origin for ramp threshold below 0·5 kg. The insert shows the same data with two additional points with ramp thresholds above 15 kg.

In order to scrutinize quantitatively the question of a possible identity or difference of the recruitment order in either modes, the correlation of the two force thresholds was worked out statistically for all pairs of motor units recorded from at any one muscle site. Thus in any such pair, the ramp force thresholds were considered to be different if their mean value calculated from ten separate trials exceeded two standard deviations, or if a t test indicated that the corresponding samples were statistically different at $P < 0{\cdot}01$; for the same pair of units, the ballistic force thresholds estimated by the method described above were considered to be different if the range of ballistic peak forces over which each unit fired insecurely (cf. Table 1) overlapped by less than one half of the smaller of these two ranges. A statistical analysis of variance of such ballistic force

TABLE 3. Statistical analysis of threshold results

5 experiments with 2 units

Ballistic recruitment	1st	2nd
2nd		4
1st	6	

Ramp recruitment

$\chi^2 = 10{\cdot}00$

$P<0{\cdot}005$

5 experiments with 3 units

	1st	2nd	3rd
3rd			4
2nd		3	
1st	8		

$\chi^2 = 30{\cdot}13$

$P<0{\cdot}005$

3 experiments with 4 units

	1st	2nd	3rd	4th
4th			0·5	2·5
3rd			2·5	0·5
2nd		2		
1st	4			

$\chi^2 = 29{\cdot}17$

$P<0{\cdot}005$

5 experiments with 5 units

	1st	2nd	3rd	4th	5th
5th					4
4th			1·5	3·5	
3rd			4·5	1·5	
2nd		3			
1st	7				

$\chi^2 = 80{\cdot}06$

$P<0{\cdot}005$

thresholds was not made since this would have required the production by the subject of well over 500 graded ballistic contractions in order to secure enough samples at any one peak force, and this would have made the whole study exceedingly cumbersome, if not impossible. Our conditions had been designed to ensure stable experimental conditions and obtain a maximum of data while avoiding deterioration through fatigue and changes in recording conditions.

The statistical relation between the two mean force thresholds is shown in Table 3. The data from experiments containing 2, 3, 4 or 5 different motor units have been tabulated separately, for the weight of the second place is not the same in a two-rank or, say, in a three-rank series (Henneman *et al.* 1965). The upper right entry in the two-by-two square of Table 3 means that, in four out of the five pairs of motor units compared, the unit with a higher ramp threshold also presented a significantly higher ballistic force threshold. The thresholds of the remaining pair of units were not significantly different both in ramp and in ballistic contractions and these two units were therefore assigned to the lower left entry, where they added to the four units of the other pairs which had a significantly lower threshold in either modes.

The five experiments with three single motor units yielded a total of fifteen comparisons. The three experiments with four units provided eighteen comparisons and the five experiments with five units gave a total of fifty comparisons by pairs. For two pairs of units which were recruited in third and fourth rank respectively in ramp contractions (significantly different thresholds), the ballistic force thresholds were undistinguishable: therefore these units were assigned half scores distributed between the shared places (cf. Henneman *et al.* 1965). Only one pair of units showed a reverse order between the two modes and exchanged third and fourth positions. The remaining eighty-five pairs of units presented the same recruitment order in the two modes, and they occupy positions along the diagonal of the squares of Table 3. The probability of a random distribution calculated from χ^2 is less than 0·005 for each of the squares of the pooled data. The rank correlation calculated according to Kendall (1962) indicated a highly consistent correlation coefficient of 0·95.

Gradation of ballistic contractions. The finding of a substantial lowering of the force threshold when the muscle is activated in the ballistic mode (Fig. 6) points to the importance of the recruitment of additional motor units at an early stage of the movement for the gradation of ballistic force. However, this is not the sole mechanism involved in tibialis anterior since, with increasing ballistic force, there occurs a definite increase in the number of discharges of each motor unit in the burst (Fig. 7*A*). The number of potentials of one motor unit can thus increase from one up to eight. The corresponding function shows a roughly linear increase with peak force up to about 10 kg (Fig. 7*A*). The maximum number of spikes in the burst ranged from 5 to 10 for the units studied over the range of forces up to about 12 kg in tibialis.

Fig. 7*B* presents for the same units the mean maximum instantaneous frequency calculated as the reciprocal of the shortest interval between two successive potentials of the units in several ballistic bursts, the peak force of which is plotted as the abscissa. This function obviously could only be estimated for ballistic contractions exceeding the ballistic force threshold of the unit considered since the latter had to discharge at least twice in the burst for allowing a frequency to be calculated (hence the data occur more to the right of the abscissa than in *A*). There is a definite trend for the maximum instantaneous frequency of each unit to increase in stronger ballistic contractions, thus providing evidence for a rate gradation mechanism. It is difficult to resolve the data into a simple function. The difficulties involved in a study of such problems at peak forces exceeding about

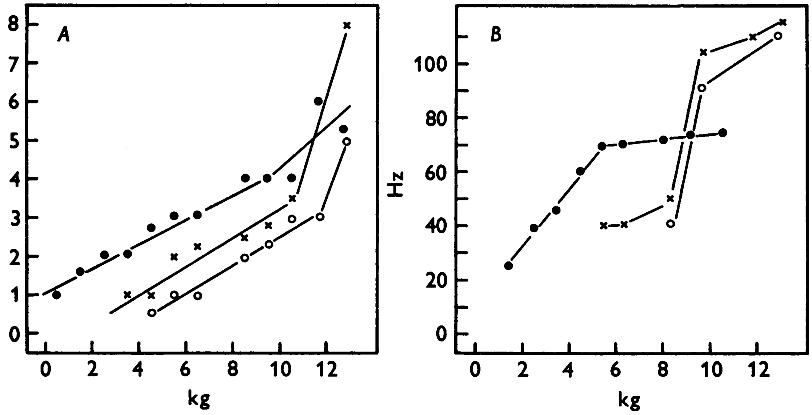

Fig. 7. Ballistic contractions of peak forces ranging from 0·05 to 12·5 kg (abscissa). *A*, number of potentials (ordinate) fired for three different single motor units in the burst corresponding to the different contractions. *B*, mean maximum instantaneous frequency at the beginning of the ballistic discharge for the same three motor units (ordinate).

12 kg (stability of the derivation, correct identification of each motor unit potential, etc.) are obvious. However there can be no doubt that, besides the obvious gradation by unit recruitment, ballistic contractions involve also a rate gradation mechanism in tibialis.

DISCUSSION

There is increasing evidence for basic differences between the motor control mechanisms involved either in voluntary smooth tracking 'ramp' contractions or in brisk ballistic contractions respectively (Kornhuber, 1971, 1974; Hopf, Lowitzsch & Schlegel, 1973; DeLong & Strick, 1974; Thach, 1975). The ballistic contractions are completed in too short a time for allowing themselves to be controlled by sensory feed-back signals from the activated muscles and the moving body parts. Therefore the corresponding cerebral motor commands must be pre-programmed and adjusted according to the expected force requirements and they must be dispatched in final form to the segmental circuits and motoneurones before the contraction is actually initiated. The present study disclosed remarkable differences in the pattern of single motor unit activation when comparing ramp and ballistic contractions. The electromyographic procedure was designed so as to present the appropriate selectivity and stability up to rather large contraction forces.

Ballistic versus ramp contractions. When the subject is tracking a slowly rising force ramp, the different motor units recorded at a single site in the tibialis are activated according to a fixed sequence, each of them starts firing when the muscle force reaches a reproducible level of force which is characteristic of that unit (Fig. 2*A*) (cf. Tanji & Kato, 1973; Milner-Brown *et al.* 1973*c*). With somewhat faster ramps the same motor units were recruited according to the same sequence, but they became active when the muscle force reached somewhat lower levels (cf. Tanji & Kato, 1973; Freund *et al.* 1975). We found that this trend was maintained during the smooth tracking of faster and faster ramps which would, for example, reach 12 kg in 0·4 sec (Fig. 3*A*). However, when the subject performed brisk contractions as fast as possible without attempting any tracking, the motor units were activated even before any force production could be recorded (Figs. 2*D*, 3*A*) and the 'threshold' could thus be said to approximate zero (Fig. 3*B*). Ballistic contractions thus involve a characteristic patterning of the motor commands with an early burst of the same motor units which had only become active at sizeable force levels during the smooth tracking of even a fast ramp. Such brisk ballistic discharge of many units abruptly throws the muscle into action and further takes advantage of a more efficient mechanical summation of the units contractions (cf. Desmedt & Hainaut, 1968). Ballistic contractions reaching their peak force in less than 0·15 sec could indeed only be achieved through a brief period of firing followed by silence since the mechanical contribution of each unit is necessarily delayed with respect to the action potential by electromechanical coupling processes and by the contraction time of the unit twitch.

Another major difference between the two modes of voluntary activation was found when plotting the instantaneous frequencies of discharge of motor units. In smooth tracking ramp contractions, the frequency of firing starts at a rather low level and it increases progressively as the muscle develops more force (Fig. 4*A*, *D*, *E*) as had already been shown for other muscles (Milner-Brown *et al.* 1973*c*). Such a progressive increase of unit frequency with force was observed even when the subject tracked rather fast ramp forces reaching, for example, 12 kg in about 0·4 sec.

A completely different pattern was recorded for the brisk ballistic contractions in which the instantaneous frequency of firing was very high (60–120/sec) at the beginning of the ballistic burst and subsequently presented a sharp drop (Fig. 4*B*, *C*). This finding points to a fundamental difference in the patterning of central motor commands in the ballistic mode.

Recruitment order in ballistic contractions. When analysing the motor units burst in strong ballistic contractions, it was found that the various units recorded at a single muscle site were with only few exceptions thrown into action in the order in which they had been recruited in a slow ramp movement (Fig. 2). This suggests that the recruitment order is generally preserved even in brisk ballistic movements. It is indeed not surprising that, in a series of trials, a motor unit would occasionally start firing ahead of another one with lower ramp threshold since the high initial frequency of discharge at the start of the ballistic burst implies a rather powerful and brisk motoneurone activation and, furthermore, because the first few motor units' potentials in such a burst are densely packed and separated by only a few msec. Thus a slight shift in the time of firing of a larger motoneurone (with a faster conducting motor axon) may well result in such occasionally different time sequences of muscle potentials in the ballistic discharges. We think that such infrequent (about 11% in 186 trials) features should not be granted undue significance and they do not justify any serious challenge of the hypothesis of a fixed recruitment order of the motoneurones (Henneman's size principle; Henneman *et al.* 1965), as was inferred by Grimby & Hannerz (1968, 1973) and Hannerz (1974) on the basis of non-systematic data.

This issue has been further clarified by devising an adequate method to estimate the ballistic force threshold of the different motor units. This was achieved by considering, not only strong ballistic contractions involving many units, but rather a large number of ballistic contractions of different peak force ranging between 0·05 and 12 kg. This allowed us to determine the smallest ballistic contraction for which any given motor unit was consistently activated (Table 1). The method allowed a reliable titration of ballistic force thresholds and showed them to be consistently related to the slow ramp force threshold (Fig. 6) ($r = 0{\cdot}92$). In the tibialis anterior muscle the force threshold of any unit is roughly reduced by a factor of 0·7 when passing from the slow ramp mode to the ballistic mode of activation. A statistical analysis by pairs of the two thresholds indicates a virtually identical recruitment order of the motor units in the two modes (Table 3). It thus appears that the motor control mechanisms programming ballistic contractions of various peak forces deal with the spinal motoneurone pool in a way which is congruent with the orderly and fixed recruitment order seen in slow ramp contractions.

Gradation mechanisms of ballistic contractions. Classical mechanisms for gradation of muscle force involve the recruitment of more units and the increase of the frequency of firing of units already active (Adrian & Bronk, 1929). In the present paper we studied voluntary contractions up to a force of 12 kg, which is about half the maximum tetanic force of the tibialis anterior in normal adults. In smooth ramp contractions the threshold of activation of single motor units were distributed over the entire range of muscle force (Fig. 6), some units being only recruited above 8 kg. The large extent of unit recruitment thresholds in ramp movements confirms data on other muscles (Tanji & Kato, 1973; Milner-Brown *et al.* 1973*c*).

In strong ballistic contractions, the same motor units discharge in an early burst and it is obvious that the recruitment of additional motor units played an important role in the force gradation (Fig. 5; Table 1). However, all the motor units studied were recruited at 5 kg peak ballistic force (Fig. 6) and the gradation of the stronger ballistic contractions must therefore depend on another mechanism, which actually involves the increase in the number of discharges of single units. Fig. 7*A* shows that this effect is quite consistently related to the peak ballistic force, since the number of spikes of individual units increased from one up to five or ten as the contraction became stronger (Fig. 5). Since the peak force is reached in less than 0·15 sec, the repetitive discharges must be accommodated in a burst of practically less than 100 msec, and the frequency indeed increases to rather high levels (60–120/sec) in strong ballistic contractions (Fig. 3*C*).

The frequency increase mechanism is perhaps less important than the recruitment of additional motor units in the gradation of ballistic movements developing small forces, as when a limb segment of finger is moved briskly under isotonic conditions without encountering any significant load. We might have failed to appreciate the full significance of the frequency coding if we had not studied strong contractions for which this mechanism assumes a crucial significance, in the tibialis muscle.

One must also consider a third feature contributing to gradation and which can only be involved in ballistic movement since it requires rather high firing rates. It is known that the excitation–contraction processes are potentiated when the activation is repeated at very short intervals in human skeletal muscles. The peak force of the contraction elicited by two stimuli at intervals from 4 to 15 msec is definitely larger than twice the force of a twitch elicited either singly or at intervals larger than about 80 msec: this force was found to be 2·4–3·2 times larger than that of the twitch in the adductor pollicis of normal man, while the rate of tension development recorded by electronic differentiation of the force signal augmented by a factor of 2·0 to 2·6 times with respect to that of the single twitch (Desmedt & Emeryk, 1968). This contractile potentiation is likely to be related to an increase in the cytostolic Ca^{2+} concentration when the subsequent muscle action potentials trigger the release of additional Ca^{2+} at a time when the sarcoplasmic reticulum has not yet removed all the free Ca^{2+} liberated by the preceding spike (Desmedt & Hainaut 1968). Another factor in this effect is that subsequent activations are more efficient to produce force when the series elastic components have been stretched by a previous contraction (cf. Close, 1972). This increase in peak tension and in rate of tension development over and above would thus enable each motor unit potential elicited at short interval in a burst to contribute more to the force and speed of the ballistic movement.

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